

A DEVELOPMENTAL ANALYSIS OF KOHLRABI AND CABBAGE STEMS¹

By A. LEON HAVIS²

Associate in horticulture, Ohio Agricultural Experiment Station

INTRODUCTION

Many horticultural and agronomic problems are concerned, either directly or indirectly, with the subject of the relative growth rates of the cells, tissues, and organs of plants. The rate of cell division in relation to rate of enlargement is a fundamental study, which when investigated more fully, should throw light on many problems concerned with the growth of economic plants. Certain physiological and nutrititional problems would doubtless be more clearly understood if more were known of the relation between cell division and enlargement and organ or body size. This field of study, in its application to agricultural research, has evidently been little investigated.

Little is now known of the relationship between genetic constitution and cell and tissue activity in any of the economic plants, except in very general terms. Such genetic interrelationships of cells and tissues within a plant organ are of primary concern in any detailed histological study of the growth phenomena in plants.

Recent studies on the relation between cell size and organ size have been concerned principally with fruits. Sinnott (4),³ however, in a study of *Acer* petioles presented results showing that organ size was to some extent directly proportional to cell size in this plant part. He also reviewed several of the earlier investigations on this subject, which show considerable inconsistency especially in general conclusions. Recent morphogenetic studies with fruits, such as those of Houghtaling (1), Sinnott (6), and Tukey (7), suggest the problem of similar growth phenomena in stems and other organs.

The study here reported was made to determine the relation between cell size and number and stem and tissue sizes in two plants closely related genetically but greatly different in stem volume, the cabbage (*Brassica oleracea* var. *capitata* L.) and the kohlrabi (*B. oleracea* var. *caulo-rapa* DC). These plants are both horticultural crops and they are of economic importance largely because of altogether different morphological developments. The terminal bud becomes the economically important or edible part of the cabbage plant; the enlarged stem becomes the edible part of the kohlrabi. The two plants are similar in their seedling stage but can be distinguished by leaf characters beyond that stage.

Based on a genetic study of cabbage and kohlrabi stems, Pease (3) concludes that the enlarged stem of the kohlrabi is determined by three multiple factors, two of which are major, the other, a minor or modify-

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³ Italic numbers in parentheses refer to Literature Cited, p. 470.

ing one. He presents no data, however, on the morphogenetic relationships of these plants, and there seems to be no literature bearing on this specific subject.

MATERIALS AND METHODS

Plants of the White Vienna variety of kohlrabi and the Copenhagen Market cabbage were used in this study. They were grown in the greenhouses of Columbia University during the fall and winter of 1939-40. Throughout most of the growing period it was necessary to lengthen days to 12 to 14 hours by the use of 500-watt lights in order to secure satisfactory thickening of the kohlrabi stem and to prevent excessive etiolation.

It is essential in such studies as these that the data be secured from comparable positions on the plant throughout growth. Under the conditions of this study, the main axes of both plants grew in height at about the same rate and reached about the same height when the rate of growth in height decreased sharply. This decrease in rate of growth indicated the time of beginning of rapid stem enlargement of the kohlrabi and relatively slow stem enlargement but rapid terminal bud development of the cabbage. The first specimens were collected at this stage of development. After considerable preliminary examination, it was found that a position about 20 mm. from the apex was most satisfactory for stem measurements in both plants throughout their development. Thereafter, studies of the growth relationships were made at very nearly that position, which was at about the center of the mature enlarged kohlrabi stem. The data presented were taken from a study of 121 kohlrabi and 48 cabbage plants. The diameter of stem of kohlrabi ranged from 1 mm. to 90 mm., the cabbage stem diameter ranged from 1 mm. to about 12 mm. All the material represented the stages from shortly after differentiation of primary tissues to approximate maturity of the stems. Because of the apparently unavoidable variation in individual plants, it seems necessary in such studies to use a large number of specimens. Uniform environmental factors are also essential.

The plant material was killed, embedded in paraffin, and cut into transverse and longitudinal sections for certain phases of the study. Most of the investigation, however, was carried out by the use of free-hand sections stained with Delafield's haematoxylin. The sections were then temporarily preserved in glycerin for examination and drawing. This latter method proved much more satisfactory, since a large number of specimens could be examined, and also because of the lack of any distortion of cells or cell walls.

The transverse plane was used in determining cell size and tissue size. Since the cells were nearly isodiametric the volume of the cells could be compared with the volume of the tissues or the stem in such a structure as the enlarged kohlrabi. A more accurate method, however, seemed to be to compare the cell diameters with the tissue and stem diameters, since the growth relations in the cabbage and kohlrabi could in this way be compared directly.

Measurements were made of the cell, tissue, and stem diameters by the use of a microprojector. These measurements were made at no less than three levels within 2 to 3 mm. of each other and averaged. Cell measurements were made in the following manner: 20 to 30 cells

in each tissue to be used were drawn under the projector and then 20 of them in each section were measured in two directions. The average of these cell diameters, carefully selected as typical, seemed reliable for this purpose. There was some variation in apparent cell sizes throughout the growth, and those measured represented the average maximum sizes shown.

The development of cell, tissue, and organ size is an exponential process; hence it is more correct to plot the growth values logarithmically. In this study, most of the plotting was done by placing the actual values on double logarithmic paper, but it was found that very wide ranges of values could be most clearly presented by the use of logarithms of actual values.

RESULTS

GENERAL STRUCTURE

The kohlrabi and cabbage stems were evidently similar in anatomy during the early stages of development. The cells within 12 mm. of the terminal meristem were almost entirely responsible for the growth in height of the plant. Those closer than 5 to 7 mm. divided rapidly; those from about 7 to 12 mm. elongated considerably. The region of differentiation seemed to lie between 12 and 16 mm. from the tip. As previously mentioned, the growth concerned in diameter relationships could best be measured at a position about 20 mm. from the tip. At 15 to 20 mm. from the terminal meristem, the pith in both plants made up 70 to 90 percent of the total stem diameter up to a diameter of 4 to 5 mm. The vascular bundles were arranged around the outside of the pith. An active cambium could be readily detected in the bundles, and in most stems there was a less active interfascicular one. The cortex, like the pith, was composed of thin-walled parenchyma during its early development. Later, collenchyma developed in the outer portion, and at near maturity, especially in the kohlrabi, an active periderm was formed in the outermost layers. The anatomy of the kohlrabi stem has been described in some detail by Vöchting (8), and it is not necessary to do so here. The writer's observations agreed with Vöchting's in all details noted.

The most striking difference between the structure of the cabbage and kohlrabi stems occurred at a stem diameter of 5 to 6 mm. At this stage an inner meristematic region developed in the center of the kohlrabi pith. Shortly after this development, four to six small vascular bundles were laid down in a circle about the group of rapidly dividing central pith cells as seen in transverse sections. As growth continued, these bundles could be seen traversing the pith in all directions, as described by Vöchting (8). Rarely were they directly associated with the larger stem bundles already mentioned. Neither this inner meristematic zone nor the medullary bundles were ever found in several other closely related plants examined, including the cabbage, cauliflower, broccoli, and brussels sprouts. In the kohlrabi they first appeared as more or less irregular strands of meristematic cells extending through the central pith. Shortly after their appearance or about the time the ring of medullary bundles was formed, the rapidly dividing cells made up a zone about 1 mm. in diameter as seen in cross section. The zone of cell multiplication enlarged toward the periphery of the pith as growth of the plant continued. At maturity it extended to

within 1 to 2 mm. of the periphery of the pith and thus made up most of the volume of the pith zone. Meristematic activity here seemed always to precede the formation of the pith bundles.

The total pith diameter made up about 90 percent of the kohlrabi and 80 percent of the cabbage stem at maturity. The edible portion of the kohlrabi was, therefore, largely of pith tissue. The bundles and cortex made up the remaining volume in about equal proportions. This study was mainly concerned with the pith, although certain relationships are given for other tissues.

GROWTH RELATIONS IN PITH OF KOHLRABI AND CABBAGE

A very definite relationship could be established between cell size and tissue size at several regions in the pith of the kohlrabi and cabbage stems by careful selection of sections at comparable positions on each plant. It is sometimes desirable to establish volume rather than diameter relationships, but here, because of the decreasing cell size as the apex is approached, it was felt that simple diameter relations at the given position (about 20 mm. from the tip) would be most accurate and comparable. The growth of the cabbage pith seemed to be mostly in width or diameter, since there was little or no increase in length at the position measured, and there was apparently only periclinal and transverse division of cells. Since the largest cells of the pith of the kohlrabi stem were nearly isodiametric and the shape of the entire stem was similar to a sphere, volume relations could be established on that basis if an accurate measure of average cell volume could be made. No method was known, however, by which an accurate volume could be obtained for cells which varied in size in different parts of both the pith and cortex and in shape during division and enlargement. Certain linear relationships, based on diameter at a definite position, could be established, however. The results from a large number of measurements show a somewhat simple growth pattern.

In order to secure a measure of the relative amount of cell division and cell enlargement during the growth of the pith, several types of measurements were made. Some of the relationships are shown in figure 1. The cell diameters of the central pith zone and the peripheral pith region were plotted against the total pith diameters on a double logarithmic grid for both kohlrabi and cabbage. The changes in relative size of the cells and the tissue can then be easily determined by measuring the ratio between the cell size and pith size at numerous stages during increase in size of the pith. This relationship can be expressed by use of the value of k ,⁴ the constant of relative growth as used by Huxley (2). If the change in relative size of cell and pith is constant and the values at different sizes are plotted against each other logarithmically, a straight line will be formed. The slope of this line which can be measured by the value of the constant, k , denotes the relationship between the two size variables. For example, if cell size is increasing at the same rate as organ size, then the line slopes upward at an angle of 45° and the value of k is equal to 1.0. If the cell size increases more slowly than the organ size, k is less than 1.0, and its

⁴ From Huxley's formula for measuring the relationship between the magnitudes of two variables. Where x is the value of the organ and y that of the varying part, the relation between them is $\log y = \log b + k \log x$, where b and k are constants. b indicates the value of y when $x=1$, and is of no importance here. The value of k denotes the relation between the two variables. This simply means that if two variables which follow this formula are plotted against each other on a double logarithmic grid their values will fall in straight lines.

value measures the relation between the two variables. If cell size is not increasing as rapidly as organ size, the difference in the relative value between them must be due to cell division. The relative amount of cell division to cell enlargement can then be calculated from the value of the relative growth constant or the relation between these two variables, or k . These relationships are, of course, independent of time and of absolute rate of growth.

As may be noted (fig. 1, *a*, *b*), growth in the central pith zone in both the kohlrabi and the cabbage was due to both cell division and cell enlargement. Cell division was responsible for most of it, however, up to a total pith diameter of about 2.2 mm., since up to this point the relative growth constant k is equal to 0.2 to 0.3. In other

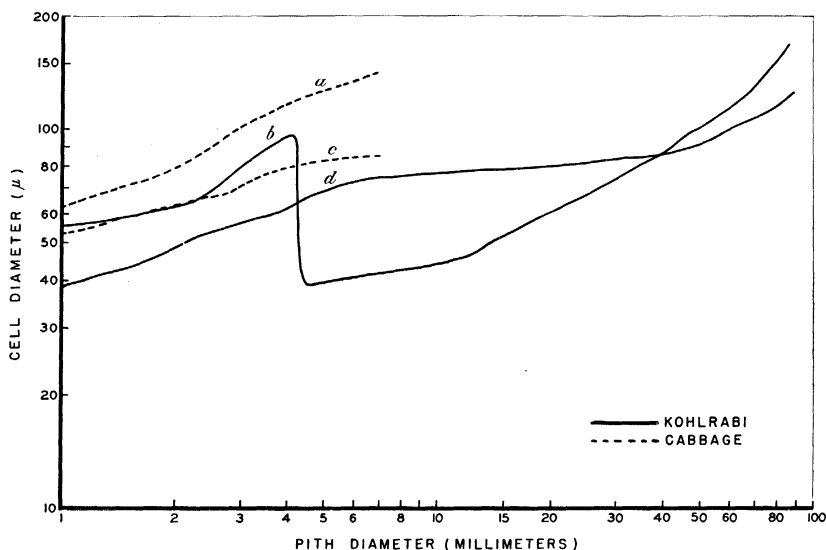


FIGURE 1.—Cell diameter plotted logarithmically against pith diameter during development of the kohlrabi and cabbage stems: *a*, *b*, Central pith cells; *c*, *d*, peripheral pith cells. The sharp break in *b* at a pith diameter of 4 to 5 mm. shows the cell relationships there at the time of development of the inner meristematic zone.

words, 20 to 30 percent of the growth was due to cell enlargement, the remainder, to cell division. At the pith diameter of about 2.5 mm., the kohlrabi central pith showed a rather sharp increase in relative rate of cell enlargement which extended to a total diameter of about 4.2 mm. At the 4.2-mm. diameter, cell enlargement was evidently responsible for about 75 percent of the growth. Cell division rate decreased at about the same stage in the cabbage, but up nearly to maturity it was responsible for about 50 percent of the increase in diameter of the pith (fig. 1). There was no sharp inflection point or position where cell division stopped and cell enlargement began.

The central meristematic zone already described appeared in the kohlrabi pith when it was between 4.0 and 4.5 mm. in diameter. With its appearance there was a sharp decrease in the average cell diameter in this region, as shown in figure 1, *b*. Thereafter, up to a

pith diameter of about 12 mm., cell division was responsible for about 80 percent of the growth in relation to the tissue as a whole. As growth continued, cell division was accompanied by more and more enlargement after each division, until at between 70 and 90 mm. in total diameter, the inner pith cells were enlarging at the same rate as the pith diameter, and $k=1.0$. Cell division evidently had then ceased, and the growth was due entirely to cell enlargement here.

The peripheral pith cells of both the kohlrabi and the cabbage were measured in successive stages of stem development in order to compare their relative rate of cell division and enlargement with that of the central cells just described. The peripheral pith cells measured were those from about the fifth to tenth cell removed from and inside the vascular bundles. The same general relationships appeared in both the kohlrabi and the cabbage up to the time of development of the inner meristematic pith zone in the kohlrabi, or to a pith diameter of about 4.5 mm. (fig. 1, *c*, *d*). Up to this point in the kohlrabi, and throughout the growth of the cabbage, the relative rate of cell division to cell enlargement was greater in the peripheral zone than in the central one. In other words, growth due to proportionately more cell enlargement occurred first in the center of the pith. From the center toward the periphery, there was a definite gradient in this type of growth which could be observed readily by microscopic examination at increasing size of the tissue. The difference in rate of cell division in proportion to cell enlargement in the two zones is well illustrated by the constantly greater value of k (fig. 1) for the central pith of the cabbage and during the early growth of the kohlrabi.

The general relationship just described was upset somewhat by the development of the central meristematic zone in the kohlrabi pith. Evidently, 60 to 70 percent of the growth at the periphery of the kohlrabi pith was due to cell division until a pith diameter of approximately 6 mm. was reached. After that size was attained there was very little change in cell size or in relative rate of cell division until rapid cell enlargement took place soon after the period of rapid enlargement of cells in the central pith just before maturity (fig. 1). The peripheral pith cells then remained larger than the inner ones throughout most of the period of enlargement of the kohlrabi stem. This is evidently a very unusual situation in plant tissues, however. In fact, examination of the cells included in the central meristematic zone showed that within it the largest cells were usually found nearest the center.

RELATIVE NUMBER OF CELLS

The regression line in figure 1 shows the relative changes in cell size at increasing kohlrabi pith size, and from these one may see where increase in cell number must be taking place most rapidly in proportion to pith size, as already described. Nevertheless, in order to clarify the relative changes in cell number, the actual number of cells can be plotted against the pith volume of the enlarged stem or "knob" of the kohlrabi (fig. 2). Because of the extreme range in number of cells, as well as in pith volume, it was more convenient to plot the logarithms of the values rather than the actual values. The measurements were made, their logarithms located on the graph paper, and then regression lines drawn through them as in the other figures.

The number of cells at any stage in the growth of the kohlrabi pith can be determined approximately by dividing the average volume of the cells into the pith volume. To determine the average volume of the pith cells, three regions were used: The center of the pith, the outermost part of the developing meristematic pith region (after it appeared), and the peripheral pith zone. The average cell volume for each was calculated on the basis of a sphere. Then a weighted average cell volume was calculated, based on the respective volumes of the inner and peripheral pith zones. The cell volume thus determined was then divided into the total pith volume, based also on a sphere. The results from 121 plants used in these determinations fit into a linear regression line (fig. 2). The logarithms of the actual values are shown, since cell number and organ volume are more nearly logarithmic or multiple, than additive relationships. Because of the

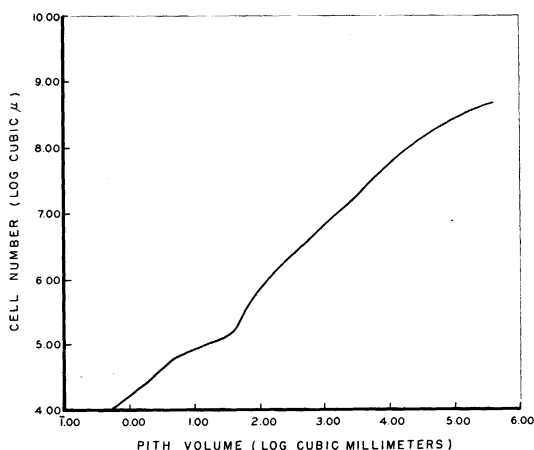


FIGURE 2.—Logarithm of cell number plotted against logarithm of pith volume in the kohlrabi stem during development of the edible portion. The sharp increase in relative cell number at a pith volume of about 1.7 marks the beginning of the rapid cell division in the inner pith.

method of calculation, these results are not as accurate as those presented in figure 1. Nevertheless, the line shows that cell number increases rapidly in the early stages of growth and increases more slowly when the pith is between 2.5 and 4 mm. in diameter. In the later stages, the advent of the central pith cell divisions was indicated by the sharp increase in cell number. The rate of increase was thereafter fairly constant until near maturity, when there was a gradual reduction in rate of increase in number of cells.

The changes in cell number in the cabbage were calculated on the basis of the diameter, that is, the number of cells across the pith in proportion to the diameter of the pith and to that of the stem (fig. 3). The line in this figure which compares the cell number to the diameter of the pith is more accurate, since the pith was growing more rapidly than the stem as a whole. If they had been growing at the same relative rate, either method of comparison would have been satisfactory. As may be noted (fig. 3), the number of cells increased at a fairly constant rate throughout the growth of the stem.

CELL RELATIONSHIPS IN THE CORTEX

The relationship between the size of the cortical cells and the size either of the organ as a whole or of the tissue itself was so variable that a graphic presentation of the results would not be very reliable. The cells varied in size considerably in different plants of the same diameter and also at different positions in the same plant. Nevertheless, measurements of cell and tissue diameters were made here with as much accuracy as feasible by the same method as used in the pith.

The cortex increased from a radius of 0.2 to 0.3 mm. when the stem was about 4 mm. in diameter to a radius of 1.5 to 2 mm. when the stem of the kohlrabi was 90 to 100 mm. in diameter. The same relationship was shown in the cabbage, but growth of the cabbage stem was limited to 12 to 14 mm. in diameter. There was much less in-

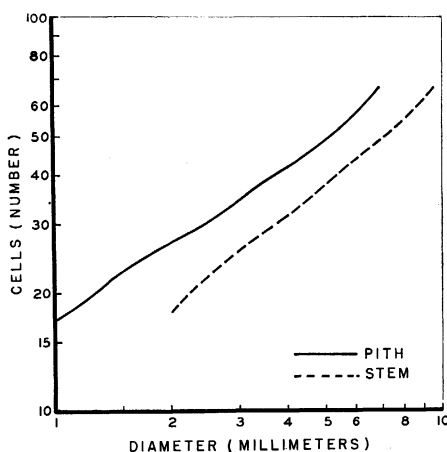


FIGURE 3.—Cell number plotted against pith and stem diameter during the increase in diameter of the cabbage stem. The number of cells represents those in a cross-section or diameter of the pith.

crease in cell size with increase in tissue size than in the pith cells. The average diameter of the cortical cells increased from about 30μ to 40μ during the development of the kohlrabi stem. Periclinal and transverse cell division persisted to maturity. The cabbage plants showed the same relationships in proportion to the diameter of the stem.

RELATIVE GROWTH RATE OF PITH AND ORGANS

The pith diameter was plotted against the total stem diameter at increasing sizes of the kohlrabi and cabbage stems in order to determine the relative growth rates of the pith and stem in these plants (fig. 4). Sinnott (5) presented results which showed that in the species he studied, the pith increased more rapidly than the remainder of the stem and that in progressively larger stems "the pith assumes an increasingly greater share of the total size and tissues outside it a smaller and smaller one." Since the pith in kohlrabi included 65 to 70 percent of the diameter of the stem when it was 3 to 4 mm. in diameter, and 90 percent of it at maturity, it is evident that the pith

increased in size more rapidly than the body or stem. Nevertheless, the relative value of this difference in the growth rate of the pith and the stem as a whole was not great. As pointed out by Huxley (2), comparatively small variations in the value of k , when plotted on a logarithmic scale, will give large differences if growth continues over a great range in size.

The value of k was determined at several regions along the regression lines (fig. 4) and for the lines as a whole. In all cases, k assumed

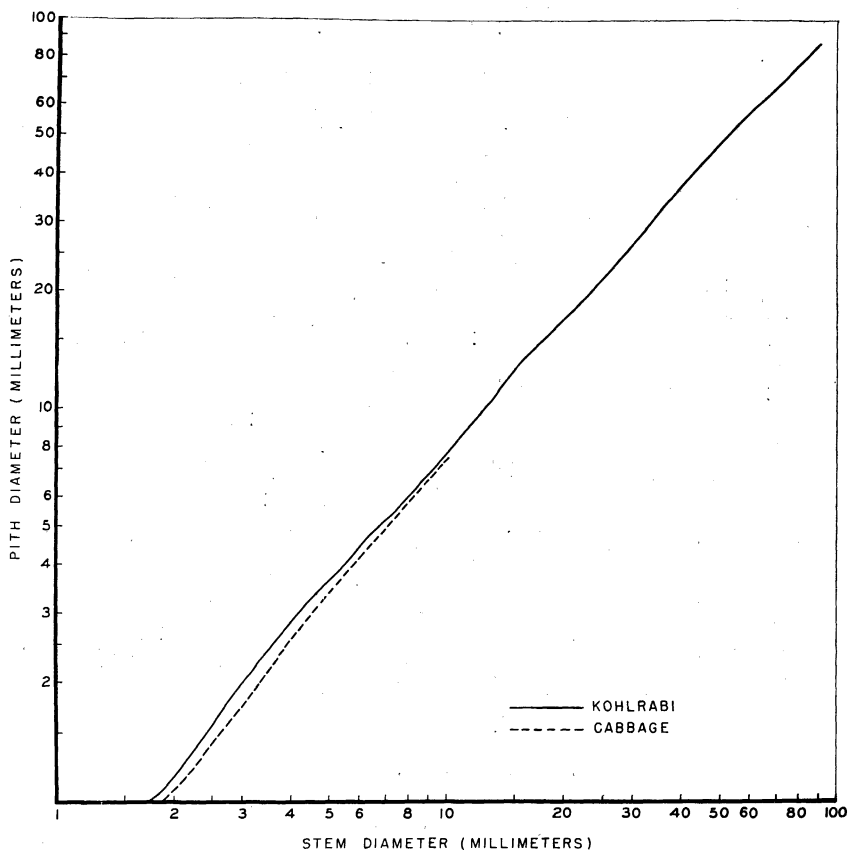


FIGURE 4.—Pith diameter plotted (logarithmically) against total stem diameter of the kohlrabi and cabbage. Both regression lines show k values of very nearly 1.1 throughout the growth of both stems.

a value of very nearly 1.1. This means that the pith was growing 1.1 times as rapidly as the stem as a whole. It might be supposed that the development of the central meristematic pith zone in the kohlrabi would increase its rate of growth in relation to the entire stem, since this zone precedes the formation of the "knob" or edible portion of the kohlrabi, which is composed of about 90 percent pith at maturity. This was not the case, however. It is especially significant that the value of k remained the same here throughout the growth of the stem in spite of the great increase in rate of cell division at the pith

diameter of about 4.5 mm. It is also significant that the growth constant k is very similar for both the cabbage and the kohlrabi (fig. 4); that is, the regression lines slope upward at the same angle. The difference, insofar as these tissue relationships are concerned, was simply in the size of the stem, not in changes in pith and stem growth relationships. In both plants, therefore, the growth of the pith has the same positive and constant differential growth relationship to organ or stem growth. In other words, the cabbage pith might become as large as that of the kohlrabi without change in its growth relationship to the entire stem; it is just a matter of extent of total growth.

GRAFTING TESTS WITH KOHLRABI AND CABBAGE STEMS

Several grafting tests were made to determine whether it was possible to affect the cell relations of either cabbage or kohlrabi stems by interchange and substitution of plant parts. For instance, it was especially desirable to know whether a cabbage stem would assume any of the characteristics of the kohlrabi if the upper portion of a plant, or that bearing the leaves, was of kohlrabi and the lower portion of the stem was of cabbage, and also whether there would be any transmission of cell and tissue characteristics if an approach graft of the stems of the two plants was made. In this way the cells and tissues of one plant could be caused to grow for a considerable distance along the stems in direct contact with those of the other plant.

It was found that cabbage and kohlrabi stems could be grafted rather easily. Several types of grafts were made at different stages of growth and at different positions on the plants. It is only necessary to state here that in no case did either plant seem to affect the cell or tissue relations in the other. In other words, the cells of each plant retained their own morphogenetic nature regardless of their relationship to cells of another genetic character. These results are, perhaps, not surprising to those who are familiar with stock and scion relations in horticultural material. Nevertheless, they seem worthy of note in view of the recent work on the relation of transfer of certain growth substances to cell activity in plants.

DISCUSSION

The results of studies of kohlrabi and cabbage stem growth are significant because the plants, which are closely related genetically, were found to be similar in certain tissue growth relationships but markedly different in others. The decrease in relative rate of cell division, first in the innermost part of the pith and then gradually toward the periphery, is notable, since the same general trend has been noted in petioles (4) and cucurbit fruits (6). As in these fruits, there was much increase in cell volume, especially in the kohlrabi pith, even during the period of cell division. The inflection point marking the end of cell division and the period of cell enlargement was not so clearly marked in kohlrabi and cabbage stems, however, as was noted in cucurbit fruits. In general, however, there was a gradual decrease in the relative rate of cell division to cell enlargement as the stems increased in size. Thus these observations and calculations show that in this pith tissue there was more and more cell enlargement after each cell division.

The development of the central meristematic zone in the pith of the kohlrabi seems remarkable, since this zone is the first to show a decreasing rate of cell division in the early stages. The medullary bundles are evidently not concerned with the initiation of this zone, since rapid cell division begins before these bundles are laid down. It is significant that as soon as these innermost cells reach a diameter of about 95μ they begin rapid division. During the growth in size of the pith, the cells farther and farther removed from the center reach that diameter, and then they start rapid division. The most peripheral pith cells do not reach 95μ until very late in the development of the stem, and this slow increase in size may be the reason why these peripheral pith cells never become extremely meristematic, as do the more central cells. The basic reason for the early difference in relative rates of cell division to cell enlargement between the central and peripheral pith cells is not clear.

In the cabbage, rate of cell division decreases first in the central pith, then in successively more peripheral cells, as in the early stages of kohlrabi growth. Its activity persists longer in the extreme peripheral pith and in the cortex (considering only the primary tissues). These results suggest that perhaps some growth substance or physiological factor associated with the bundles might be responsible for the delay in maturity of nearby cells. Such a factor would not explain the condition in the pith of the older kohlrabi, however, where the central meristematic zone develops.

That there is no relationship between cell division and total growth of pith size in proportion to stem size is well illustrated in this study. In spite of the advent of the very meristematic zone in the kohlrabi pith, the same rate of growth relative to the stem as a whole obtains here as in its earlier growth, and as in the cabbage stem. The morphogenetic difference between the kohlrabi and the cabbage stems seems to be due largely to the persistence of cell division, accompanied by cell enlargement, to a greater stem size before growth ceases. The difference is also partly due to the greater size finally attained by the kohlrabi pith cells.

It may be concluded that there are several morphogenetic factors involved in the development of size differences in the stems of closely related plants. Thus, the genetic factors concerned with histological development are responsible for several definite structural differences between the cabbage and kohlrabi stems. Some of these can be measured by a quantitative analysis of structural changes during the course of development.

It would seem that a more fundamental solution to many horticultural problems could be obtained if more were known of the histological development of the plants or plant parts concerned. More might be known also about the influence of different practices or treatments on the relative rates of cell division and cell enlargement and on tissue and organ size relationships.

SUMMARY

In developing kohlrabi and cabbage stems cell diameter in the pith and cortex was compared with pith and also with stem diameters.

The greater size of the kohlrabi stem was due largely to a greater number of cells, although some of the difference was evidently due to cell size.

The pith, of which the edible kohlrabi is largely composed, grew at the same rate, relative to the entire stem, throughout its development, and at the same relative rate as that of the cabbage pith to its stem.

There was no sharp point of demarcation between the cell division stage and the cell enlargement stage in the growth of the pith and cortex of these stems.

The innermost cells of the pith increased most rapidly in size, and, in the kohlrabi, were the first to become very meristematic again after a definite size was reached.

By use of grafting tests with kohlrabi and cabbage stems, it was found that the cells of each plant retained their own morphogenetic nature even though they developed in direct contact with each other.

Some factors involved in the histological differences between the stems of the two plants are discussed.

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